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THE INHERITANCE OF CONGENITAL CATARACT IN CATTLE[1]

CATARACT in mammals may be due to environmental causes, or it may be hereditary. The mode of inheritance has been debated. In the case of man Bateson (1) and Davenport (2) regarded cataract as a dominant Mendelian character, while Jones and Mason (3) in an analysis of human pedigrees collected by Harmon (4) concluded that cataract is probably a simple recessive. Danforth (5) raised some pertinent objections to this latter hypothesis, and Jones and Mason (6) later admitted the validity of some of these objections. There are a number of elements in this analysis of human pedigrees which are no doubt perplexing, but the preponderance of evidence seems to favor the hypothesis that cataract in man is a Mendelian recessive.[2] Hereditary cataract is known in some mammals other than man, but little is known regarding its transmission. Hurst (8) stated that liability to cataract-blindness in horses is a Mendelian character.

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[1] Paper No. 10 from the Laboratory of Genetics, Illinois Agricultural Experiment Station.

[2] The data as analyzed by Jones and Mason seem convincing because of the large value of P, a measure of goodness of fit of the observed to the calculated series. While there can be little doubt but that the observed results lie within reasonable limits of error when tested by any one of several approved methods, it should, perhaps, be stated that Jones and Mason's use of Pearson's criterion is hardly justified, inasmuch as Pearson's formula applies to a correlated system of variables in which the sum of the observed frequencies = sum of calculated frequencies, and the sum of the errors = 0. Harris (7) pointed out the value of Pearson's formula in relation to Mendelian ratios. Now in any complex Mendelian ratio of the form $(\frac{1}{2}+\frac{1}{2})^n$ or $(\frac{3}{4}+\frac{1}{4})^n$ where $n =$ the number of allelomorphic pairs and where all terms of the ratio are given, the above conditions are always met. However, the observed series which Jones and Mason attempted to fit to a calculated series is neither a complete Mendelian ratio nor does it fulfill the conditions stated. Jones and Mason were not satisfied with the goodness-of-fit value when the heterozygotes were mated *inter se* ($P = 0.418$), but if the deviations were due to random sampling we should expect the values of P to fluctuate around 0.5. Their results would therefore be interpreted as consistent with their theory, if their method were correct. By using the method adopted by Jones and Mason, one might nevertheless obtain a better (?) fit in this case and thus a more satisfactory result if one dealt with the series of normals in this population rather than the series of cataractous. In any monohybrid ratio, the deviation of the dominant class is equal to the deviation of the recessive class. Hence, if we divide the same series of deviations all the way through by a series of larger calculated values for normals, then X^2 will be perceptibly smaller and P larger ($P = 0.71$ in this case). This procedure would be somewhat comparable to stating that in a single toss of 8 coins, 5 heads are more likely to appear than 3 tails, or in a single throw of n coins (n–p) heads are more probable than p tails.

The data forming the basis of this paper arose through the circumstance that a registered Holstein-Friesan bull, E. T. H. (Holstein-Friesan Herdbook No. 62924) transmitted desirable economic dairy characters to a marked degree, and consequently attempts were made to fix his characters by inbreeding. A number of cataractous offspring resulted from these close matings. The simultaneous occurrence of several cataracts in the progeny of a single bull could not be attributed to chance environmental or intrauterine conditions; hence the pedigrees of all animals involved were carefully studied. There was no record of cataract in any of the ascendants. The original bull, E. T. H., had been mated to a large number of unrelated cows and produced 93 normal F_1 offspring. Thirty-two of these F_1 daughters were mated to an F_1 son and produced 63 F_2 calves, of which 55 were normal and 8 showed well-defined congenital cataracts of the stellate type.[3] The ophthalmological aspects of these cases have already been described by Small (8).

Cataract is evidently *recessive* in cattle and if it is a simple Mendelian recessive then the original progenitor, E. T. H., was heterozygous, Nn, where N = normal and n = cataractous. Mated to unrelated normal females, NN, we should expect the 93 F_1 offspring to be perfectly normal, but of two genetic types in equal numbers, NN + Nn. In selecting any F_1 son to breed to the F_1 daughters, it was equally probable that he would be either a homozygous normal, NN, or a heterozygous normal, Nn. A single F_1 son, also a registered Holstein-Friesan bull, V. H. (Holstein-Friesan Herdbook No. 158293), was chosen and he proved to be heterozygous. Since half of the F_1 daughters were homozygous and half were heterozygous, the former would produce gametes, N + N, and the latter would produce gametes, N + n. The total population of F_1 daughters would therefore produce three times as many normal as cataractous gametes. In Mendelian notation the F_1 matings were as follows:

$$\tfrac{3}{4}\text{N} + \tfrac{1}{4}\text{n} = \text{gametes from } F_1 \text{ females,}$$

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[3] The writers are indebted to Dr. C. P. Small, of Chicago, Illinois, for identifying the type of cataract and for much additional information, and wish to express their appreciation of the deep interest Dr. Small has shown in this case.

$$\tfrac{1}{2}\mathrm{N} + \tfrac{1}{2}\mathrm{n} = \text{gametes from } \mathrm{F}_1 \text{ males,}$$
$$\underbrace{\tfrac{3}{8}\mathrm{NN} + \tfrac{4}{8}\mathrm{Nn}}_{\text{normal}} + \underbrace{\tfrac{1}{8}\mathrm{nn}}_{\text{cataractous}} = \mathrm{F}_2 \text{ zygotes.}$$

That is, $\frac{7}{8}$ of the F_2 calves should be normal and $\frac{1}{8}$ should be cataractous. The observed results agree with the calculated rather better than one would usually expect, for the observed = 55 normal + 8 cataractous and the calculated = 55.125 normal + 7.875 cataractous. The 8 F_2 cataractous calves were of both sexes (2 heifers and 6 bulls).

All these facts clearly indicate that the original sire, E. T. H., was heterozygous, Nn. If mated to his own daughters he should give results similar to those of his son, V. H. He was thus tested and produced 7 offspring of which 3 (1 bull and 2 heifers) were cataractous. Collecting all matings of the sire, E. T. H., and his son, V. H. (both were Nn) to F_1 daughters (NN + Nn) we found:

	Normal	Cataractous	Total
Observed	59	11	70
Calculated	61.25	8.75	70

We may therefore conclude that congenital cataract in cattle is a simple recessive Mendelian character.

To prevent the reappearance of cataractous individuals in this stock and to reduce the proportion carrying cataract as a recessive is a matter of some economic importance. After all cataractous individuals have been eliminated, there still remain one half of the daughters and four sevenths of the granddaughters of E .T. H. which carry a recessive factor for cataract. We can not distinguish between the NN and Nn individuals, since N is evidently dominant to n. Whatever the proportion of these two types may be to each other, mating the cows to normal unrelated bulls (which are almost unquestionably NN) will eventually reduce the cataractous-bearing individuals to a negligible minimum. If we begin with r + s individuals of the genetic constitutions NN and Nn respectively, and we back cross to normal stock, NN, any number of times, p, then the genetic composition of the last generation produced after p such back crosses will be

$$[2^p r + (2^p - 1)s]\mathrm{NN} + s\mathrm{Nn}.$$

Since the first term becomes much larger than the second as p increases, the number of homozygous normals becomes very great compared with the heterozygous normals.

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FURTHER OBSERVATIONS ON SEX IN MERCURIALIS ANNUA

IN an earlier paper,[1] I briefly mentioned the occurrence of so-called monœcious forms in *Mercurialis annua.* I have since then continued my studies upon such forms and this report deals with the offspring of the so-called monœcious plant, No. 3. It is to be noted that *Mercurialis annua* is described as appearing in

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[1] Inheritance of Sex in *Mercurialis annua, American Journal of Botany,* Dec., 1919.